

Research article

Beach-cast seagrass wrack contributes substantially to global greenhouse gas emissions

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ABSTRACT

Seagrass ecosystems have received a great deal of attention recently for their ability to capture and store carbon, thereby helping to mitigate climate change. However, their carbon-sink capacity could be offset somewhat if exported plant material – which accounts for ~90% of total leaf production – undergoes microbial breakdown and is emitted into the atmosphere as a greenhouse gas. Here we measured emissions (CO_2 and CH_4) from the breakdown of exported seagrass plant material, focusing on beach-cast ‘wrack’. We tested two seagrass species; *Zostera nigricaulis* and *Amphibolis antarctica*, which have contrasting morphologies and chemistries. We found that both species of wrack were substantial sources of CO_2 , but not CH_4 , during the decomposition process. Biomass loss and the coinciding CO_2 emissions occurred over the 30-day experiment, and the pattern of CO_2 emissions over this time followed a double exponential model ($R^2 > 0.92$). The initial flux rate was relatively high, most likely due to rapid leaching of labile compounds, then decreased substantially within the 2–9 days, and stabilizing at $< 3 \mu\text{mol g}^{-1} \text{ d}^{-1}$ during the remaining decomposition period. Additionally, seagrass wrack cast high up on beaches that remained dry had 72% lower emissions than wrack that was subjected to repeated wetting in the intertidal zone. This implies that relocation of seagrass wrack by coastal resource managers (e.g. from water's edge to drier dune areas) could help to reduce atmospheric CO_2 emissions. Scaling up, we estimate the annual CO_2 -C flux from seagrass wrack globally is between 1.31 and 19.04 Tg C yr⁻¹, which is equivalent to annual emissions of 0.63–9.19 million Chinese citizens. With climate change and increasing coastal development expected to accelerate the rate of wrack accumulation on beaches, this study provides timely information for developing coastal carbon budgets.

1. Introduction

Seagrass beds are highly productive coastal ecosystems, with annual seagrass production estimated at 1 kg DW m^{-2} per year (Duarte and Chiscano, 1999). Despite covering only 0.15% of global sea surface area, these ecosystems contribute approximately 1% of the net primary production of the global ocean (Duarte and Cebrian, 1996). Roughly half of this seagrass biomass is in the above-ground biomass, and is mainly composed of leaf and stem material (Duarte and Chiscano, 1999; Hemminga and Duarte, 2000). The lifespans of seagrass leaves are on average 90 days (Hemminga et al., 1999), while rhizome life-spans can range from days to years (Hemminga and Duarte, 2000). Duarte and Chiscano (1999) estimated seagrass above-ground biomass turnover rate to be 2.6% of total standing stock per day. As a result of

this high turnover rate, detached seagrass biomass that is subsequently transported by wind and current dynamics (Mateo, 2010; Jiménez et al., 2017) may result in large amounts of seagrass wrack accumulation along coastlines globally (Colombini and Chelazzi, 2003; Cardona and García, 2008; Macreadie et al., 2017) (Fig. 1).

Seagrass wrack has many important ecological functions, providing food and habitat for sandy beach fauna (Ince et al., 2007; Lewis et al., 2007), nutrients for dune vegetation (Cardona and García, 2008; Del Vecchio et al., 2017), and protection for coastal dunes (Kirkman and Kendrick, 1997; Dugan et al., 2003). Nevertheless, seagrass wrack is often considered a nuisance to humans due to the production of unpleasant odors when wrack mattes decompose on the shoreline (Hansen, 1984; Kirkman and Kendrick, 1997). This decomposition process also coincides with the production of carbon (C) emission

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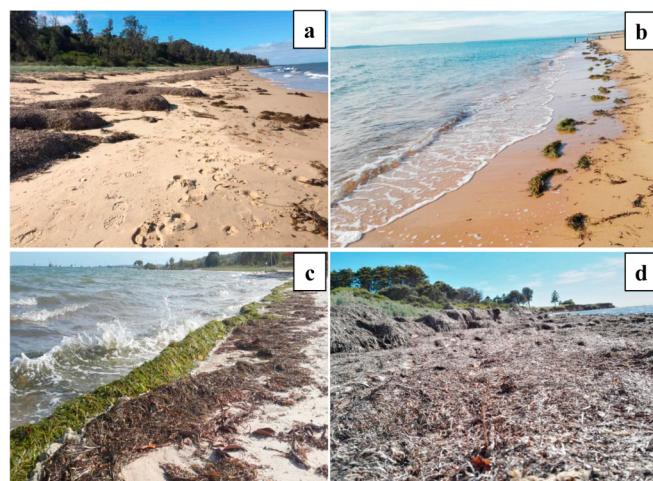


Fig. 1. Examples of seagrass wrack distribution: on the slope of a sandy beach (a), near the shoreline (b, c), and away from shoreline (d), as well as seagrass wrack deposits at a beach outside the Hastings yacht club (Victoria, Australia). (photographs by S. Liu and P. I. Macreadie).

hotspots (greenhouse gas, GHG) in coastal habitats (Coupland et al., 2007). Coupland et al. (2007) reported that if left on the beach, seagrass wrack has an approximate emission rate of $6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. However, thus far the GHG emission production of the accumulated seagrass wrack has only been measured at a single time point, leaving a significant gap in what is known about how GHG emissions vary during the seagrass wrack decomposition process.

Seagrass wrack deposited along the coast is exposed to periods of wetting through tidal inundation, and can be redistributed locally by storm and wind action (Coupland et al., 2007) (Fig. 1). The seagrass wrack accumulating near the water's edge is more likely to retain moisture due to tidal inundation (Fig. 1c), while seagrass wrack accumulating away from water's edge is exposed to relatively dryer conditions (Mateo et al., 2006; Coupland et al., 2007; Cardona and García, 2008) (Fig. 1d). Moisture can accelerate the decomposition of plant wrack by facilitating the loss of soluble compounds through leaching and enhancing the activity of decomposers (Dick and Osunkoya, 2000; Nicastro et al., 2012), which ultimately results in elevated GHG flux (Sayer et al., 2011; Liu et al., 2017). For example, Coupland et al. (2007) found that the macrophyte wrack near the water's edge showed much higher CO_2 fluxes ($\sim 6\text{--}12 \mu\text{mol m}^{-2} \text{ s}^{-1}$) than those further away from the water's edge ($\sim 2\text{--}3 \mu\text{mol m}^{-2} \text{ s}^{-1}$). However, empirical evidence of how moisture influences seagrass wrack decomposition and thus GHG emissions is otherwise rare.

Seagrasses globally are diverse in their inherent structure and chemistry, which could influence their decomposition. Trevathan-Tackett et al. (2017a) has found that morphologically larger taxa have the potential to contribute more refractory organic matter to vegetated coastal ecosystems, i.e., Posidoniaceae > Zosteraceae in temperate seagrass families. de los Santos et al. (2012, 2016) have reported that high lignocellulose content of seagrass tissues usually corresponding to low consumption and high breaking force, with important implications of low decomposition rate. Furthermore, the decomposition rate of rhizome and root tissues, always with more lignocellulose content than leaf tissues, are significantly lower than those of leaf tissues (Fourqurean and Schrlau, 2003; Vichkovitten and Holmer, 2004). For example, only 5% of the original mass of *Thalassia testudinum* leaves remained, compared to 49% of rhizome after 348 days of decomposition (Fourqurean and Schrlau, 2003). As such, decomposition rates of seagrass wrack are influenced by seagrass species chemistry and tissue proportions, and consequently may result in different GHG emission potential.

Here we performed a laboratory experiment to test how the inherent

seagrass characteristics (i.e. morphology and chemistry) and position on the beach (moisture content) affect GHG emission rates. We chose the common beach-cast seagrass species *Amphibolis antarctica* and *Zostera nigricaulis* that have contrasting morphologies (*Amphibolis* spp. have long vertical rhizomes) (Lavery et al., 2013), and chemistries (*Zostera* spp. wrack generally has more labile organics and high decomposition rates) (Cebrián et al., 1997; Trevathan-Tackett et al., 2017a). We aimed to use the different species with distinct chemistry and tissue proportions to explore the contribution of beach-cast seagrass wrack to GHG emissions under wet and dry conditions by estimating the possible range of GHG emission potential. The results from this study will help estimate the possible GHG emissions from seagrass wrack, as well as provide a basis for creating useful solutions for reducing GHG emissions for resource managers.

2. Materials and methods

2.1. Experimental design and sampling

In April 2017, we collected freshly deposited, green *A. antarctica* (from outside the Sommers yacht club, 38.39° S , 145.15° E , VIC, Australia) and *Z. nigricaulis* (from outside the Hastings yacht club, 38.30° S , 145.19° E , VIC, Australia) wrack, which was distributed near the water's edge. During collection, seagrass samples with no visual signs of decomposition (no discoloration, intact leaves and stems) were targeted to ensure seagrass tissues were fresh with minimal decomposition occurring prior to laboratory incubations. The *A. antarctica* seagrass wrack was composed of leaves and stems, while the *Z. nigricaulis* wrack was only composed of leaves. *In situ* seawater was collected and all the materials were transported directly to the laboratory.

Before the experiment, the seagrass wrack was washed with the seawater, and a separate representative subset of seagrass wrack was dried to a constant weight in order to calculate the wet weight:dry weight (WW:DW) conversion of the two seagrass species. For the decomposition experiment, 50 g wet weight (approximately 6 g and 15 g dry weight for *Z. nigricaulis* and *A. antarctica*, respectively) seagrass wrack was placed on plastic trays ($n = 6$ and $n = 8$ for *Z. nigricaulis* and *A. antarctica*, respectively). Seagrass replicates for each species were divided into a wet group ($n = 3$ or 4, sprayed with seawater taken from the collection site) and a dry group ($n = 3$ or 4, without spray). To generate the wet treatment, we used a spray bottle of seawater (taken from the collection site) to spray about 10 ml onto the seagrass wrack once a day to mimic a tidal regime. We used 400 W metal-halide lamps fitted with light diffusing covers to mock the summer sunlight: daytime from 5 a.m.–8 p.m. and nighttime from 8 p.m.–5 a.m. All samples were exposed to $29 \pm 0.5^\circ \text{ C}$ temperatures in the daytime and $18 \pm 0.4^\circ \text{ C}$ temperatures at night for 30 days. Meanwhile, we checked the seagrass wrack every day to insure that the invertebrates had never been observed in the lab. At selected times (days 0.125, 0.25, 0.5, 1, 2, 4, 6, 9, 14, 22 and 30), CO_2 and CH_4 fluxes were measured. After the 30-day incubation, the seagrass wrack was dried to a constant weight and the dry mass measured.

2.2. Sample analysis

CH_4 and CO_2 fluxes at each selected time were measured using an LGR™, Ultra-Portable Greenhouse Gas Analyzer (UGGA, Model 915-0011, Los Gatos Research, Palo Alto, CA, USA) with a 0.2 Hz sampling rate, connected to a transparent Licor (LI-8100A) automated soil CO_2 Flux System (chambers 160 height \times 200 mm diameter). The chambers were clamped closed and connected to the UGGA for 8 min to allow changes in CH_4 and CO_2 concentration to stabilize within the chamber headspace. Before each measurement, CH_4 and CO_2 concentration were recorded to correct for ambient levels in the laboratory (i.e. blanks). Measurements of CH_4 and CO_2 concentrations in parts per million (ppm) were taken at 5 second intervals over the 8 minute

contact period (96 individual measurements per sample). The linear rate of change in chamber gas concentration (ppm s^{-1}) was then used in the following equation (Lambert and Fréchette, 2005):

$$k = \left(\frac{\delta \times c1 \times c2 \times v}{m} \right) \times c3 \quad (1)$$

where k represents the flux rate of gas from the seagrass wrack surface to the atmosphere ($\mu\text{mol g}^{-1} \text{DW d}^{-1}$), δ represents the slope of change in chamber gas concentrations over time (ppm s^{-1}), $c1$ represents the conversion factor from ppm to $\mu\text{g m}^{-3}$ (655.47 for CH_4 and 1798.45 for CO_2), $c2$ represents the conversion of seconds to days (86400), v represents the volume of air within the chamber (m^3), m represents the seagrass wrack DW (g), and $c3$ represents the conversion from μg to μmol (0.0625 for CH_4 and 0.022722367 for CO_2). Temperature and ambient pressure were automatically incorporated by the UGGA.

The linear change in gas concentration was individually assessed and R-squared values were used as a form of quality control for the selection of fluxes incorporated into the analysis (all R-squared (R^2) values were 0.88 or above). In this study, we did not detect changes in CH_4 concentration.

The carbon (C) and nitrogen (N) concentrations within the biomass of dry seagrass wrack were measured both before and after the incubation experiment. This was achieved by grinding seagrass biomass to below a size of 0.15 mm (#100-mesh size), and then passing the materials through an Elemental CHNS analyzer model Vario EL cube (Vario EL, Elemental Analyzer systeme GmbH, Germany).

2.3. Data analysis

Data were first tested to meet the assumption of homogeneity of variance, and where heterogeneity of variance was found, data were log transformed. The linear mixed model (seagrass species and moisture treatments were fixed effects) was used to test for significance for the following variables: (a) seagrass biomass remaining, (b) wrack biomass C loss, (c) total C emitted as CO_2 (CO_2 -C flux), (d) proportion of CO_2 -C flux to biomass C loss (CO_2 -C flux/biomass C loss) and (e) initial total wrack C (CO_2 -C flux/initial total wrack C). Next, post-incubation seagrass wrack characteristics were compared between wet and dry groups within each seagrass species by using a student's t -test. A correlation analysis was determined between the CO_2 flux and biomass C loss. A two-way analysis of covariance (ANCOVA) was used to analyze the effects of seagrass species and moisture treatments on CO_2 flux rate with time as a covariate. Lastly, a one-way ANCOVA was used to analyze the effects of moisture on the CO_2 flux rate with time as a covariate within each seagrass species. The species and moisture effect with $\alpha < 0.05$ was considered statistically significant. Additionally, different functions, including linear, exponential, logarithmic, polynomial, hyperbola, power and parabola functions, were applied to the CO_2 flux rate of seagrass wrack to find the model of best fit (the highest R^2 value). All above mentioned statistical analyses were performed with SigmaPlot 12.0 (Systat Software Inc., Chicago, IL), IBM SPSS Statistics 19.0 software (IBM SPSS Statistics 19, IBM Corporation, Somers, NY) and Microsoft Office Excel 2007 (Microsoft Corporation, Redmond, WA).

3. Results

3.1. Characteristics of seagrass wrack

The mean elemental C and N content of *Z. nigricalis* and *A. antarctica* wrack at the beginning of the incubation were 30.1% C and 1.85% N, and 30.1% C and 0.92% N, respectively. After 30 days of decomposition, seagrass biomass loss was significantly influenced by moisture (Table 1, $p = 0.003$) but not species (Table 1, $p = 0.534$), with the wet group losing ~6% more biomass than the dry group (Table 2). The results also showed that the remaining C content of the wet group

Table 1

Statistical analysis of the effects of the seagrass species and moisture treatments on seagrass remaining biomass and CO_2 -C flux parameters using the linear mixed model (two seagrass species and two treatments as the fixed effects). Values reported are F -statistics.

Parameters	Species	Moisture	Species × Moisture
Remaining biomass	0.415	15.995**	2.968
Biomass C loss	100.668***	147.487***	0.045
CO_2 -C flux	98.477***	225.448***	8.009*
CO_2 -C flux/biomass C loss	0.719	0.676	1.921
CO_2 -C flux/initial total wrack C	98.533***	225.452***	8.019*

* $0.01 < p \leq 0.05$; ** $0.001 < p \leq 0.01$; *** $p \leq 0.001$.

was significantly lower than the dry group (Table 2). The biomass C loss was calculated based on the variations of the biomass and C content after the incubation. The biomass C loss within the wrack tissue was significantly influenced by species (Table 1, $p < 0.001$) and moisture (Table 1, $p < 0.001$; Fig. 2). In addition, the biomass C loss of the wet group was significantly higher than the dry group within the respective seagrass species (Fig. 2; *Z. nigricalis*, $t = 17.869$, $p < 0.001$; *A. antarctica*, $t = 7.613$, $p = 0.004$).

3.2. Characteristics of CO_2 flux

In this study, only CO_2 emissions were detected during wrack decomposition, while CH_4 flux was below the detectable limit. The CO_2 flux rates of *Z. nigricalis* and *A. antarctica* were about 250 and 80 $\mu\text{mol g}^{-1} \text{DW d}^{-1}$, respectively, at the beginning of the incubation. These values then decreased to 3.4 and 1.6 $\mu\text{mol g}^{-1} \text{DW d}^{-1}$ by the end of the experiment, respectively. The CO_2 flux rates initially decreased sharply in the first two days and then became stable for the dry groups, while for the wet groups the flux rates declined over the nine-day period (Fig. 3). Seagrass species (two-way ANCOVA, $F = 54.522$, $p < 0.001$) and moisture treatments (two-way ANCOVA, $F = 29.897$, $p < 0.001$) significantly influenced the CO_2 flux rate. CO_2 flux rates of *Z. nigricalis* were observed to be generally higher than that of *A. antarctica* (Fig. 3). Meanwhile, significantly higher CO_2 flux rates were observed in wet groups compared to dry groups for both *Z. nigricalis* (one-way ANCOVA, $F = 12.48$, $p = 0.001$; Fig. 3a) and *A. antarctica* (one-way ANCOVA, $F = 63.366$, $p < 0.001$; Fig. 3b). Furthermore, the CO_2 flux rates of the two seagrass species in both treatments were best fit to double exponential functions (Fig. 3 and Table 3; in all cases $R^2 > 0.92$, $p < 0.001$).

According to the fitted double exponential functions for CO_2 flux rates, the definite integrals ranging from 0 to 30 were calculated to estimate total C emitted as CO_2 (CO_2 -C flux) during the 30 days of decomposition (Fig. 4). CO_2 -C flux was significantly different between seagrass species (Table 1, $p < 0.001$) and moisture treatments (Table 1, $p < 0.001$), with presented markedly interactive effects of seagrass species and moisture as well (Table 1, $p = 0.021$). In the wet groups, the CO_2 -C flux of *Z. nigricalis* (1.39 $\text{mmol g}^{-1} \text{DW}$) and *A. antarctica* (0.72 $\text{mmol g}^{-1} \text{DW}$), were 3-fold and 6-fold higher than their dry groups, respectively (Fig. 4; *Z. nigricalis*, $t = 10.062$, $p = 0.001$; *A. antarctica*, $t = 10.751$, $p < 0.001$).

CO_2 -C flux/initial total wrack C ratios was significantly influenced by seagrass species (Table 1, $p < 0.001$), moisture treatments (Table 1, $p < 0.001$) and these interaction effects (Table 1, $p = 0.020$) but not the CO_2 -C flux/biomass C loss ratios (Table 1; species, $p = 0.416$; moisture, $p = 0.430$; species × moisture, $p = 0.227$). There was a significantly higher CO_2 -C flux/initial total wrack C ratio in the wet group than the dry group within each seagrass species (Fig. 5a; *Z. nigricalis*, $t = 10.062$, $p = 0.001$; *A. antarctica*, $t = 10.751$, $p < 0.001$), with the CO_2 -C flux only accounting for 0.41%–5.95% of the initial total wrack C (Fig. 5a). Additionally, the CO_2 -C flux was much lower than the total biomass C loss (Fig. 4 vs. Fig. 2); however, the CO_2 -C flux/biomass C

Table 2

The elemental content and remaining biomass of seagrass wrack after 30 days of decomposition (mean \pm S.E.M.). The asterisks in the dry group indicate values are significantly higher than the wet group for each seagrass species (Student's t-test, $p < 0.05$).

Parameters	<i>Zostera nigricaulis</i>		<i>Amphibolis antarctica</i>	
	Wet group	Dry group	Wet group	Dry group
Remaining Biomass (%)	79.3 \pm 2.7	85.8 \pm 1.6*	83.7 \pm 1.1	87.8 \pm 0.81*
C (% DW)	22.7 \pm 0.43	26.6 \pm 0.40**	27.3 \pm 1.1	32.9 \pm 0.20***
N (% DW)	1.40 \pm 0.030	1.52 \pm 0.04	0.690 \pm 0.026	0.76 \pm 0.052
C/N	18.9 \pm 0.070	17.1 \pm 0.8	46.5 \pm 1.9	51.0 \pm 3.8

*0.01 $< p \leq 0.05$; ** 0.001 $< p \leq 0.01$; *** $p \leq 0.001$.

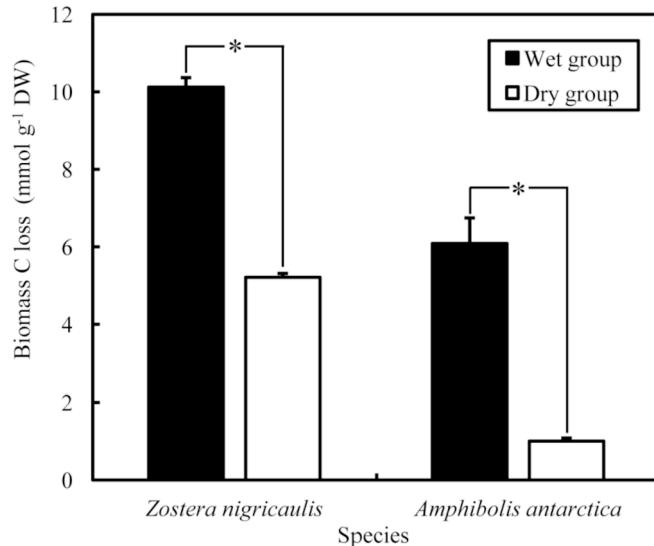


Fig. 2. The biomass C loss of *Z. nigricaulis* and *A. antarctica* wrack after 30 days of decomposition. Values were calculated by normalizing the g of biomass lost to the shift in %C during decomposition, and were converted to match the flux units. The asterisks above bars indicate a significant difference between the wet group and dry group within the same seagrass species (Student's t-test, $p < 0.05$).

loss ratio was similar between the wet and dry groups of both seagrass species (average proportion $\sim 12\%$; Fig. 5b). Furthermore, the CO₂-C flux had a significantly positive correlation with biomass C loss (Fig. 6).

4. Discussion

The elemental C and N content and C/N ratio of collected *Z. nigricaulis* and *A. antarctica* wrack were similar to values of living tissues (Walker and McComb, 1988; Pedersen et al., 1997; Hirst et al., 2016; Hirst and Jenkins, 2017), indicating the collected seagrass wrack was fresh prior to the laboratory incubation. After 30 days' incubation, the remaining biomass of *Z. nigricaulis* wrack was 83%, which was consistent with previous studies that found 60–90% of *Zostera* spp. biomass remained after 30 days of decomposition (Bourguès et al., 1996; Vähdälä and Søndergaard, 2002; Dye, 2006). The per day loss rate of *A. antarctica* wrack ($0.47\% \text{ d}^{-1}$) in this study was lower than other known decay rate for *A. antarctica* ($0.58\text{--}0.65\% \text{ d}^{-1}$) (Walker and McComb, 1985; Moore and Fairweather, 2006). As Enríquez et al. (1993) reported that plant wrack decomposition rates were strongly positively correlated with the initial nitrogen concentration of the wrack, the slower rate may be due to the inclusion of *A. antarctica* vertical rhizomes in this study; stems typically, have higher C/N ratios than leaves (Walker and McComb, 1988).

The ratios of remaining biomass and biomass-C loss were dependent on the seagrass characteristics prior to decomposition. *A. antarctica* wrack had a relatively large proportion of vertical rhizome material

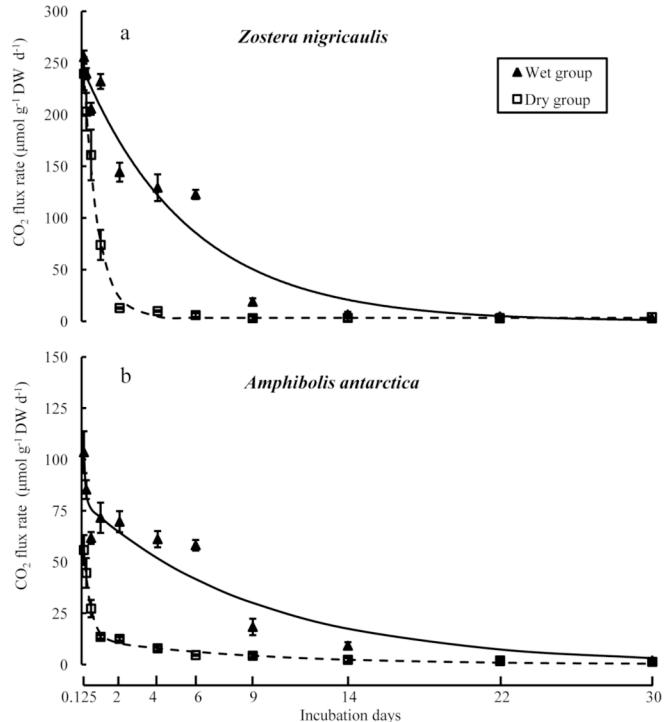


Fig. 3. The CO₂ flux rate of *Z. nigricaulis* (a) and *A. antarctica* (b) during the 30-day incubation. Values represent means \pm S.E.M.

Table 3

Double exponential function fitted to the CO₂ flux rate over 30 days of decomposition. x = time in days; y = CO₂ flux rate ($\mu\text{mol g}^{-1} \text{ DW d}^{-1}$).

Species	Treatment	Model equation
<i>Zostera nigricaulis</i>	Wet group	$y = 243.6473e^{-0.176x} + 89.8074e^{-12.4185x}$, $R^2 = 0.9563$
	Dry group	$y = 3.3094e^{-2.0571E-18} + 282.6102e^{-1.3329x}$, $R^2 = 0.9961$
<i>Amphibolis antarctica</i>	Wet group	$y = 114.661e^{-12.2325x} + 80.0313e^{-0.1088x}$, $R^2 = 0.9337$
	Dry group	$y = 12.9597e^{-0.1237x} + 62.4327e^{-2.8276x}$, $R^2 = 0.9959$

(Lavery et al., 2013), while the *Z. nigricaulis* wrack was predominantly made up of leaf biomass. *Z. nigricaulis* plants do have stems at maturity, however the stems were not present during the initial wrack collection, suggesting a relatively more consistent contribution of their leaf compared to stem biomass in wrack production at the site or time of collection. In general, the vertical rhizomes of *A. antarctica* are highly lignified and contain large amounts of well-structured vascular tissue compared to leaves (Lavery et al., 2013). Furthermore, the C/N ratios of *Z. nigricaulis* and *A. antarctica* wrack were 19 and 38 at the beginning of the experiment, respectively. The lower initial nitrogen concentration

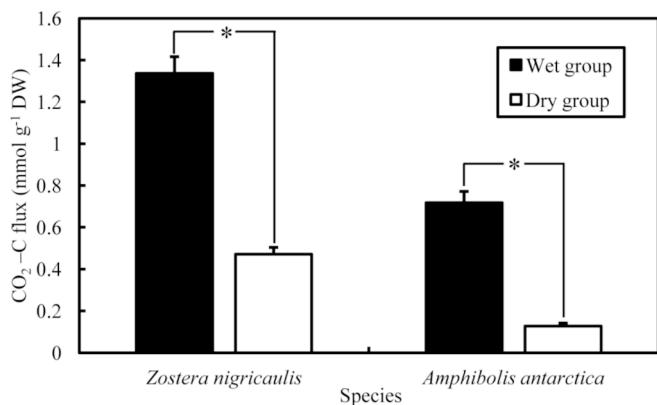


Fig. 4. The accumulative C as CO₂ flux (CO₂-C flux) from *Z. nigricaulis* and *A. antarctica* during 30-day incubation. The asterisks above bars indicate significant difference between the wet group and dry group within the same seagrass species (Student's *t*-test, *p* < 0.05). Values represent means \pm S.E.M.

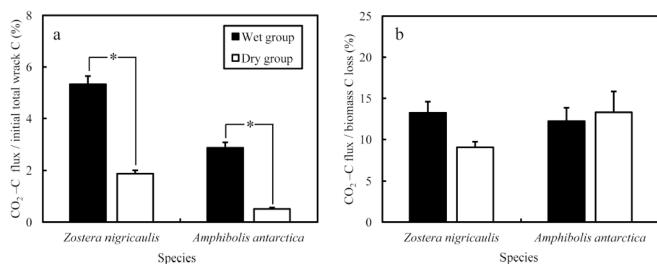


Fig. 5. The percentage of CO₂-C flux to the initial total wrack C (a) and CO₂-C flux to biomass C loss (b) after 30-day incubation. The asterisks above bars indicate significant difference between the wet group and dry group within the same seagrass species (Student's *t*-test, *p* < 0.05). Values represent means \pm S.E.M.

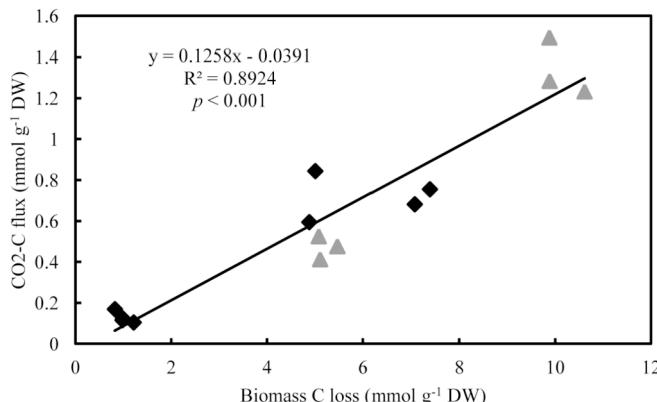


Fig. 6. Relationship between the biomass C loss and CO₂-C flux. Gray triangle and black diamond symbols represent the *Z. nigricaulis* and *A. antarctica* data, respectively.

frequently correspond to slower decomposition rates (Enríquez et al., 1993), which may explain the differences of the relatively low decomposition rates and biomass C loss of *A. antarctica* compared to *Z. nigricaulis*. In addition to lower biomass and C loss, we found a significantly lower CO₂ flux rate and CO₂-C flux for *A. antarctica* compared to *Z. nigricaulis* wrack. This aligns with previous work suggesting that the biomass C loss of seagrass wrack is rapidly utilized by microbes (Harrison and Mann, 1975; Peduzzi and Herndl, 1991), which can generate CO₂ through respiration (Vichkovitten and Holmer, 2004; Liu et al., 2017), but is also influenced on inherent chemical make-up of the plant (Trevathan-Tackett et al., 2017a).

Environmental conditions also significantly influence GHG emission of the decomposing seagrass. By simulating different positions of the beach-cast seagrass wrack at the water's edge, we showed that more frequently wet conditions enhanced wrack decomposition, as demonstrated by the significantly higher rates of biomass and C loss compared to dry wrack in this study. These results are also supported by previous studies (Schimel et al., 1999; Chen et al., 2000; Nicastro et al., 2012). For example, there was a 27% longer half-life of *Z. muelleri* litter decomposing in the high intertidal than litter decomposing in the low intertidal and subtidal zones (Nicastro et al., 2012). There are two mechanisms behind this increased decomposition. First, moisture can enhance the loss of soluble materials via leaching (Swift et al., 1979; Nicastro et al., 2012); and second, moisture can provide more suitable conditions for microbial breakdown of seagrass tissue (Schimel et al., 1999; Chen et al., 2000; Dick and Osunkoya, 2000). As a result, it is likely that the elevated CO₂ flux rate in wet seagrass wrack treatments in this study is attributed to higher microbial respiration and leaching (Schimel et al., 1999; Chen et al., 2000). These results provide empirical evidence of the impact of moisture on CO₂ emissions from seagrass wrack.

The pattern of CO₂ flux rate also indicated that there was variability in GHG emissions during the decomposition process. The double exponential function had the best fit for describing the patterns in the CO₂ flux rate ($R^2 > 0.90$), indicating that there were two distinct phases of CO₂ emissions from the wrack samples. This is consistent with the 2-phase patterns found for seagrass biomass decay (Fourqurean and Schrlau, 2003) and the dissolved organic carbon (DOC) leaching rate model (Maie et al., 2006; Lavery et al., 2013). The high initial CO₂ emission rate is likely due to the abundant initial labile compounds leaching from fresh dead material, which act as a resource for microbial metabolism (Peduzzi and Herndl, 1991; Vähtälö and Sondergaard, 2002; Lavery et al., 2013). Subsequently, we recorded a sharp decrease in CO₂ flux rate over time, which likely indicates a concomitant reduction in the DOC leaching rate (Maie et al., 2006; Lavery et al., 2013; Liu et al., 2017). Therefore, these data show that moisture facilitated microbial activity and the DOC leaching of wrack, which resulted in relatively higher CO₂ flux rates that lasted 4-fold longer than dry decomposition conditions.

Although we only measured the CO₂ flux rate during a 30 day period, the CO₂ flux rate was below 3 $\mu\text{mol g}^{-1} \text{DW d}^{-1}$ at the end of the incubation. Thus, we used the 30 days' integral of fitting double exponential function to estimate the CO₂-C flux potential is reasonable. At a global scale, seagrass meadows produce large amounts of beach wrack, which in turn could generate large amounts of CO₂. Beach-cast seagrass wrack is mainly composed of leaf material, with the exception of *Amphibolis* spp., which also contains a large proportion of vertical stem material (Lavery et al., 2013). The seagrass leaves of different species have similar labile and recalcitrant carbon compositions compared to other seagrass tissue types (Trevathan-Tackett et al., 2017a). Additionally, the significant interaction effect of species and moisture treatments on CO₂-C flux suggested that wet condition could enhance CO₂-C flux to a greater extent of *Z. nigricaulis* wrack than that of *A. antarctica* wrack. The seagrass vertical rhizomes have lower CO₂ flux potential than leaf material, as discussed above, which could help determine the possible range of CO₂ emissions from seagrass wrack. According to the data presented here, the CO₂-C flux/initial total wrack C ratios ranged between 0.41% and 5.95%. It has been estimated that the annual seagrass net primary production to be 490 Tg C yr⁻¹, with the fraction ending up as wrack being approximately 320 Tg C yr⁻¹ (subtracting burial and grazing pathways) (Duarte, 2017; Duarte and Krause-Jensen, 2017). Furthermore, most seagrass wrack follows the decomposition pathway with only a small fraction of seagrass wrack directly consumed by animals (Duarte and Cebrian, 1996; Duarte and Krause-Jensen, 2017). Therefore, if we assume that most of the seagrass wrack enters decomposition, the annual CO₂-C flux of seagrass wrack can be roughly estimated as 1.31 to 19.04 Tg C yr⁻¹ globally. This rate

is equivalent to annual emissions of 0.63–9.19 million Chinese citizens (Hertwich and Peters, 2009). Using a similar approach, the average annual CO₂-C fluxes were 3.53 and 12.54 Tg C yr⁻¹ under dry and wet conditions, respectively, based on the mean CO₂-C flux/initial total wrack C ratios in the dry and wet conditions (3.92% and 1.10%, respectively). While our estimate is based on only two seagrass species from one region of the world and should therefore be considered a ‘back of the envelope’ estimate, it certainly suggests that GHG emission potential from wrack is of global significance. Furthermore, we have shown dried wrack lead to a 72% decrease in CO₂-C flux compared continually wet wrack. Based on these findings, we suggest that removal of seagrass wrack from the water’s edge and relocation to drier environments (e.g. upland dune areas) may provide a practical approach for resource managers to reduce emissions of CO₂ and limit global warming. However, seagrass wrack can provide food and habitat for invertebrates and birds (Ince et al., 2007; Lewis et al., 2007), as well as nutrients for nearby vegetation (Cardona and García, 2008; Del Vecchio et al., 2017). Therefore, the seagrass wrack ecology function should be taken into account when the resources managers put the removal of seagrass wrack into effect.

In this study, we found that the biomass C loss was much higher (~85%) than the CO₂-C flux recovered. The deficit in C recovery may be due to several factors. First, the biomass C loss may have been overestimated because of difficulties with sampling-fragmented detritus. Second, during the decomposition period, seagrass wrack C would have been rapidly transformed into microbial biomass (Peduzzi and Herndl, 1991; Vähätalo and Søndergaard, 2002; Lavery et al., 2013). Lastly, leaching of carbonate and the process of photooxidation of organic C to carbonate is also possible during the wrack decomposition process (Anesio et al., 1999). These two scenarios, although not measured here, could be important alternative or unaccounted for pathway for C transformation, since the transformation of C into microbial biomass and photooxidation of organic C could represent 8–13% and 23–30% of the loss C during decay, respectively (Peduzzi and Herndl, 1991; Vähätalo et al., 1998; Vähätalo and Søndergaard, 2002). Additionally, the CO₂-C flux showed a significantly positive correlation with biomass C loss, which accounted for about 12% of the biomass C loss across both seagrass species and moisture treatment. This finding indicates that the CO₂-C flux of seagrass wrack is directly related to the biomass C lost as a result of decomposition. Since seagrass species have different decomposition rates (Harrison, 1989), this estimate would provide useful in estimating the CO₂ emission potential of seagrass species that decompose rapidly (e.g., *Halophila decipiens* (7.1–11% loss d⁻¹; Harrison, 1989)) or more slowly (e.g., *Posidonia australis* and *Heterozostera tasmanica* (0.1–0.5% loss d⁻¹; Harrison, 1989)). Besides moisture, many other environmental factors such as temperature (Trevathan-Tackett et al., 2017b), oxygen (Godshalk and Wetzel, 1978), and solar radiation (Vähätalo et al., 1998) can also affect seagrass decomposition. For future research, we recommend investigating the drivers of GHG emissions for common wrack-producing seagrass species during decomposition on the shoreline in order to help estimate the CO₂ flux potential more accurately, and further assist to tip the coastal GHG budgets towards net sequestration.

5. Conclusion

This study suggests that beach-cast seagrass wrack can be a globally-significant contributor to greenhouse gas emissions. Using wrack with contrasting chemistries and tissue components, we estimated that the annual global CO₂-C flux of seagrass wrack is estimated between 1.31 and 19.04 Tg C yr⁻¹, which is equivalent to annual emissions of 0.63–9.19 million Chinese citizens. As dry conditions can lead to a 72% decrease in CO₂-C flux compared to wet conditions, we recommend (where practical) that the relocation of beach-cast seagrass wrack from wet conditions (low intertidal) to drier areas (e.g. dune areas away from tidal/wave influence) may help to reduce emissions of CO₂. Our study

also shows that decomposition potential differs by seagrass species (Harrison, 1989), and many environmental variables, temperature, oxygen and solar radiation, can affect seagrass wrack decomposition (Godshalk and Wetzel, 1978; Vähätalo et al., 1998; Trevathan-Tackett et al., 2017b). We recommend further research into species-specific CO₂-C flux potential, and its response to a range of environmental factors.

Author contributions

SL, STT, XH and PIM conceptualized and designed this study. SL, CJEL, QRO, STT and PM performed the experiments. SL, ZJ and XH performed data analysis. All authors contributed to the writing of the manuscript. All authors have read and approved the final version of the manuscript.

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